

VIII. Gynandromorphous *Agriades coridon*, *Poda*; *A. coridon ab. roystonensis*, *Pickett*. By E. A. COCKAYNE, D.M., F.R.C.P., F.E.S.

[Read March 1st, 1916.]

PLATES LXV-LXXIII.

THREE forms of *Agriades coridon* occur, in which the blue scaling differs in amount on the corresponding wings on the two sides. In females, which have a good deal of blue on the hind-wings, it is not very unusual to find the blue spots larger on one side than on the other, or to find one or more diffuse patches or well-defined spots on one hind-wing unrepresented on the other. In the second of these forms one finds one or even more than one streak of brilliant blue scales. Such streaks are generally confined to one wing, and are seen more often on the fore-wing than on the hind-wing. The specimen figured is exceptional in having the fore-wing and the hind-wing on opposite sides affected in this way. Both these forms are referable to *ab. inaequalis*. Tutt, but they are probably due to different causes and for this reason deserve distinctive names. I propose to restrict the name *ab. inaequalis* to the second, or streaked form (Pl. LXXII, figs. 1 and 2), and to name the first or unequally spotted form *ab. impar* (nov. ab.), (Pl. LXXIII, figs. 1 and 2). The majority of specimens described as gynandromorphous in the lists of Oscar Schultz are examples of *ab. inaequalis* in this restricted sense, but it is doubtful if there is really a male element in them or in *ab. impar*. Though I have examined a number of well-marked specimens of both forms I have never seen androconia in either, except in a specimen which shows gynandromorphism on the right side and a blue spot without androconia on the left. This specimen affords strong evidence of the different nature of the asymmetry of blue scaling in *ab. impar* and *ab. roystonensis*.

In the third form, with very few exceptions there is inequality in the size of the wings, and the blue scales are accompanied by androconia and coarse hair scales. In my article on these specimens with asymmetry of size and

blue scaling, published in the "Entomologists' Record," 1914, I stated that they also fell under Tutt's ab. *inaequalis*. Mr. Pickett has written recently at some length to prove that this is not so, and has named the form ab. *roystonensis*, extending it to include specimens with inequality in the size of the corresponding wings, but without asymmetry of blue scaling. He says that Tutt had never seen a specimen of ab. *roystonensis*, but a reference to "British Butterflies," vol. iv, shows that this is not strictly accurate. On p. 6 of this work Tutt describes a specimen taken by Dr. Hodgson in 1888 near Brighton as a teratological example ( $\theta\theta$ ), and refers both to the extra blue scales and to the smaller size of the blue-scaled wings. On p. 30, where he describes ab. *inaequalis*, he specially refers to it as an example of the aberration. Fortunately I have examined it microscopically, and have seen androconia and coarse hair scales on the smaller right fore-wing and androconia on the smaller hind-wing. Like the Royston specimens it is undoubtedly gynandromorphous.

In the "Entomologists' Record," 1914, I gave descriptions of six complete dissections of Royston gynandromorphs, and in the Journal of Genetics, 1915, I described a seventh. On this rather meagre material I ventured to make some generalisations, for which I hoped to obtain further support at a later date. This I have been enabled to do by fresh material obtained in 1915 by my own efforts and through the kindness of my friends.

In this paper I propose to discuss these peculiar gynandromorphs, including all specimens coming under Pickett's ab. *roystonensis*, with a complete account of my new dissections, dealing with them under the following headings.

1. *Geographical range.*
2. *Family and hereditary character.*
3. *Anatomy of internal and external genitalia.*
4. *Psychology.*
5. *External appearance.*
6. *Theoretical discussion.*

#### GEOGRAPHICAL RANGE.

The vast majority have been taken at Royston on the borders of Hertfordshire and Cambridgeshire, where they

occur year after year. They are very scarce, and, since they cannot be distinguished in flight from normal females, they may be overlooked very easily. I estimated roughly that one was present in every 2000 females, and Pickett says he took 66 amongst 60,000 females, or approximately one in 900.

Mr. P. M. Bright has a specimen taken at Tring in 1899. Mr. A. E. Gibbs made a preliminary investigation of the Tring and Dunstable chalk hills in 1915, and, although the weather was very unfavourable, two specimens were captured near Dunstable. I examined the Tring and Dunstable specimens, and found that they agreed with Royston examples in having the wings on one side smaller than those on the other and dusted with blue scales, coarse hair scales and androconia.

These specimens from such outlying localities in Hertfordshire and Bedfordshire suggest that wherever *coridon* occurs in these counties gynandromorphs of this kind will be found. The only specimen, of which I have certain knowledge, taken outside these counties is the one already mentioned in the Hodgson Collection at Cambridge, set on a gilt pin and labelled "Bevingdean, 7. 9. 1888." According to Tutt this is Bevendean near Brighton. The gynandromorphous specimen captured by Briggs on the Sheep Leas, Horsley, Surrey (*Entom.*, xx, p. 266), is stated by Tutt to be female on the left side and male on the right side, with the *wings slightly smaller on the male side*. This reduction in size of the wings on the male side makes it probable that this is an instance of the same phenomenon.

The great excess of females over males at Royston has led to the suggestion that there may be a connection between it and the prevalence of the preponderantly female gynandromorphs. Some evidence of this may be obtained by noting whether it occurs at Tring and Dunstable and elsewhere in Hertfordshire, and in the Brighton district.

#### FAMILY AND HEREDITARY CHARACTER.

We know that gynandromorphism of various kinds may be familial or hereditary. Though direct proof that it is familial is lacking in the case of the Royston gynandromorphs, there is circumstantial evidence in favour of its being so. They are so rare that one may search for a

whole day or more examining thousands of females and not find a single gynandromorph, and then one may find two or three close together in a very short time.

This fact has been noticed by Mr. Newman and Mr. Pickett, both of whom have collected very extensively at Royston, and by other Entomologists. My own experience strongly supports the view that several may occur in one family.

In 1914, one evening when *coridon* was beginning to settle down for the night, I found two on neighbouring plants of knapweed, and two others only a few yards away. All four were very perfect and probably had emerged quite recently.

Last year I had a still more striking experience. I went to the locality too early in the season and found that *coridon* was scarce and that few females had emerged. Mr. Newman told me that in three days he had not captured a single gynandromorph. Yet on July 25th, in one small, rather isolated piece of ground, where not more than fifty females were flying, I took five gynandromorphs, and a sixth specimen with the wings smaller on one side but without any blue sealing. All these had emerged quite recently, and none had ova descending the oviducts. Two other gynandromorphs were taken elsewhere on the downs. On July 28th I took a specimen with one side small and with two blue scales and a coarse hair scale on the small side on the same bit of ground, and on August 1st took four more gynandromorphs and another female with the wings unequal, but with only two blue scales on the small side, all on exactly the same spot. Prolonged search elsewhere only yielded two more. All the ones taken close together were very freshly emerged, and were probably members of a single family.

In describing the internal and external organs in this species I have continued to use the names adopted in my earliest papers. Dr. Chapman, however, has very kindly written to me and told me that he considers the organ I have named the *caput bursae* to be the entire *bursa copulatrix*, and that what I call the *bursa copulatrix* is nothing more than a specialised chitinous arrangement for extruding the long tubular prop or hypostema with its chitinous genital opening. He names this the rein or henia. His views are probably correct. But the subject is a difficult one, as it is uncertain what structures in

the Plebeid Blues are homologous with those found and named by Pierce and Burrows in the *Noctuidae* and *Geometridae*, and, indeed, whether the prop and rein have any homologues in these classes. Under these circumstances I must be content to leave my diagrams to show my meaning without in any way insisting on the correctness of my nomenclature.

#### ANATOMY OF INTERNAL AND EXTERNAL GENITALIA.

The following are descriptions of eighteen gynandromorphs, fourteen examined in a fresh condition, four after preservation in spirit, all taken at Royston in 1915. For the four specimens in spirit I am indebted to Mr. H. B. Williams. There are also descriptions of four specimens with inequality of size, but without androconia on the small side. Three had one or two blue scales on the small side, the fourth had none and is, I believe, unique. The specimen described by Pickett as having no blue scales has at least one.

No. 1. Fore-wings, right 16 mm. in expanse, left 15 mm. Discal spots ringed with white on both sides, ab. *albicincta*, Tutt. Many blue scales on right fore- and hind-wings, numerous androconia and coarse hair scales. Ovaries and cement glands equal and normal. Spermatheca present. *Caput bursae* (*bursa copulatrix*, Chapman) and *ductus seminis absent*. Rein and prop present. External genitalia symmetrical and like those of normal female.

No. 2. Fore-wings, right 13.75 mm., left 14 mm. Blue scales with numerous androconia and coarse hair scales on left fore-wing. Underside ab. *parisiensis*, Gerh., on both sides. Ovaries and cement glands equal in size and normal. *Bursa copulatrix*, *caput bursae*, *ductus seminis* and *spermatheca* normal. *Caput* contained much dark-coloured material. External genitalia symmetrical and like those of normal female.

No. 3. Fore-wings, right 16.25 mm., left 15.75 mm. Underside almost symmetrical. Discal spots on upperside ringed with white, pale blue wedges internal to lunules on both hind-wings. Many blue scales and androconia on left fore- and hind-wings, coarse hair scales on left fore-wing. Ovaries symmetrical. *Caput bursae* of abnormal shape (Fig. 4). *Ductus seminis* represented by a blind remnant leading from common oviduct. *Cement gland on left side small, on right side almost entirely aborted* (Fig. 5). *Spermatheca* normal. *Caput bursae* empty. External genitalia symmetrical and like those of normal female.

No. 4. Fore-wings, right 15 mm., left 16 mm. Underside colour and spotting symmetrical. Blue scales with numerous androconia and coarse hair scales near apex and along posterior margin of right fore-wing. Blunting of apex. Only two or three blue scales on right hind-wing. Ovaries and cement glands symmetrical. Other organs present and normal. Caput bursae contained much dark material. External genitalia symmetrical and like those of normal female.

No. 5. Fore-wings, right 14.5 mm., left 16 mm. Blue scaling diffuse but slight on both wings on right side. Androconia numerous. Underside alike on both sides. Ovaries and cement glands symmetrical. Other organs normal. Caput contained a little granular material. External genitalia symmetrical and like those of normal female.

No. 6. Fore-wings, right 17 mm., left 15.5 mm. Underside colour and spotting symmetrical. Blue scales, coarse hair scales and androconia numerous along posterior border of left fore-wing, diffuse blue scaling on left hind-wing. Ovaries normal and symmetrical. *Cement glands* symmetrical but *small*. Bursa, caput and ductus seminis normal, *spermatheca nodular* (Fig. 6).

No. 7. Fore-wings, right and left 13 mm., hind-wings, right 11 mm., left 10 mm. No blue scales on fore-wings, dense patch of blue scales with androconia near anal angle of left hind-wing, and reduction of lunules. Slight asymmetry of spotting on underside. Ovaries small but symmetrical; cement glands normal and symmetrical. Bursa, caput, ductus seminis and spermatheca normal. Caput empty. External genitalia symmetrical and like those of normal female (Pl. LXVII, fig. 2).

No. 8. Fore-wings, right 16.5 mm., left 15 mm. H.B.W. Diffuse but thin blue scaling over wings on left side. Numerous coarse hair scales and androconia. Lunules small on left hind-wing. Upperside colour and underside colour and spotting alike on both sides. Ovaries and cement glands normal and symmetrical. Other organs present and normal. *Caput bursae* empty and *abnormal in shape* (Fig. 2). External genitalia symmetrical and like those of normal female.

No. 9. Fore-wings, right 16 mm., left 17 mm. H.B.W. Extensive diffuse blue scaling with numerous androconia on both wings on right, coarse hair scales numerous on right fore-wing. General facies the same on both sides. Ovaries and cement glands normal and equal. *Caput bursae and ductus seminis absent*. Rein and prop present. Other organs present and normal. External genitalia symmetrical and those of normal female.

No. 10. H B W. Wings smaller on right but too little difference



to measure accurately. Small patch of blue scales with many androconia near apex of right fore-wing, numerous blue scales and androconia on right hind-wing with smaller lunules. General faecies alike on the two sides. Ovaries and cement glands normal and symmetrical. Bursa, caput and ductus seminis normal. Caput empty. *Spermatheca branched* (Fig. 7). External genitalia symmetrical and like those of normal female.

No. 11. Fore-wings, right 16 mm., left 17 mm. H.B.W. General faecies alike on both sides. Blue scales most numerous near posterior margins of fore- and hind-wings on right. Androconia numerous. Lunules on right hind-wing reduced. Ovaries and cement glands normal and symmetrical. Other organs present and normal. Caput empty. External genitalia symmetrical and like those of normal female.

No. 12. Fore-wings, right 15.5 mm., left 16 mm. Costa o right fore-wing curved. General faecies alike on both sides, discal spots ringed with white, ab. *albicincta*, Tutt. Diffuse blue sealing of both wings on right. Lunules reduced. Androconia and coarse hair scales few in number. Ovaries and cement glands large and symmetrical. Other organs present and normal. Caput empty. External genitalia symmetrical and like those of normal female.

No. 13. Fore-wings, right 15 mm., left 16 mm. General faecies alike on both sides. Blue scales diffuse but not numerous on both wings on right. Androconia numerous even amongst purely brown scales. Ovaries and cement glands normal and symmetrical. Other organs present and normal. Caput bursae full of dark material. External genitalia symmetrical and like those of normal female.

No. 14. Fore-wings, right 16 mm., left 15 mm. Blue scales, coarse hair scales, and androconia numerous on the left fore-wing, local patch of blue scales without androconia on the left hind-wing. No reduction in size of lunules. General faecies alike on both sides, underside near ab. *parisiensis* on both sides. Ovaries and cement glands normal and symmetrical. Other organs present and normal. Caput empty. External genitalia symmetrical and like those of normal female.

No. 15. Fore-wings, right 13 mm., left 13.5 mm. Right fore-wing: numerous blue scales, coarse hair scales and androconia diffused over surface. Right hind-wing has only about 33 blue scales with one androconial scale. General faecies the same on both sides. Ovaries and cement glands symmetrical and normal. Other organs present and normal. Caput empty. External genitalia symmetrical and like those of normal female.

No. 16. Fore-wings, right 16.4 mm., left 15.5 mm. Stripe of

densely packed blue scales, coarse hair scales and androconia on left fore-wing. No blue scales on left hind-wing. Ovaries and cement glands symmetrical and normal. Other organs present and normal. Caput empty. External genitalia symmetrical and like those of normal female (Pl. LXV, fig. 1).

No. 17. Fore-wings, right 16.5 mm., left 17.5 mm. Facies alike on both sides, very dark colour. Very small patch of blue scales, coarse hair scales and androconia along posterior border of right fore-wing. The patch is only just visible to the naked eye. No blue scales on right hind-wing, but obvious reduction in total area and in size of lunules. Ovaries and cement glands symmetrical and normal. Other organs present and normal. Caput contains granular material. External genitalia symmetrical and like those of normal female (Pl. LXVIII, fig. 2).

No. 18. Fore-wings, right 16.25 mm., left 14 mm. Left hind-wing smaller than right. Upperside facies the same on both sides. Underside, right typical, left ab. *parisiensis*. Left antenna shorter than right. Left fore-wing has one blue scale near apex and a blue scale and coarse blue hair scale near posterior border. No androconia seen. Ovaries and cement glands symmetrical and normal. Other organs present and normal. Caput empty. External genitalia symmetrical and normal (Pl. LXXI, fig. 2).

No. 19. Both wings smaller on the left side, right fore-wing 17 mm., left 16 mm. General facies alike on both sides. One blue scale external to discal spot on small fore-wing. Lunules slightly reduced on small hind-wing. Internal and external genitalia like those of normal female.

No. 20. Both wings smaller on the right. Internal and external genitalia like those of normal female.

No. 21. Fore-wings, right 17.25 mm., left 16.5 mm. Very dark specimen. Marked reduction of size of lunules on the small left hind-wing. Careful microscopic search revealed no blue scales and no androconia. Ovaries and cement glands equal in size and large. Other organs present and normal. Caput contained granular material. External genitalia symmetrical and like those of normal female (Pl. LXIX, fig. 2).

In addition to above complete dissections partial examinations were made of sixteen gynandromorphs, taken in August and September 1915 at Royston by Mr. I. W. Newman, and set and dried by him in the usual way. They were treated with potash, and though minor abnormalities may have been overlooked an almost perfect dissection was carried out on some of them. In seven,



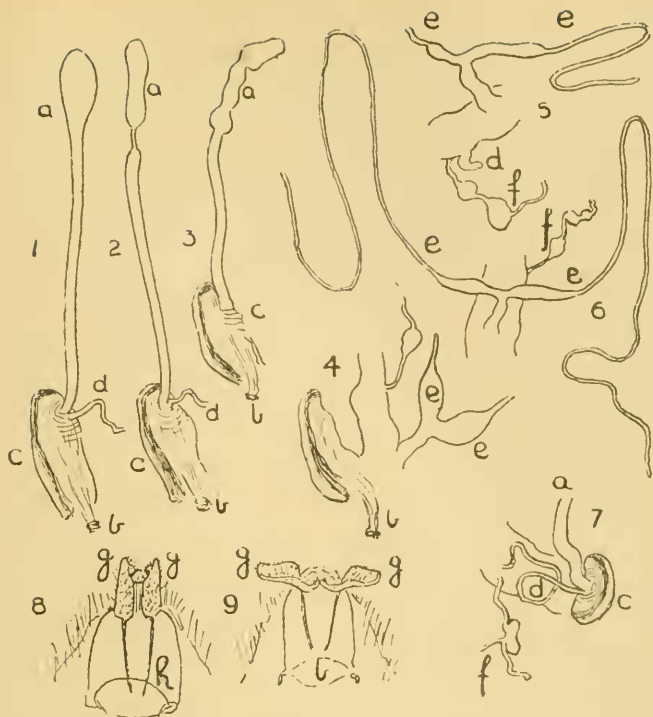


FIG. 1.—Normal bursa copulatrix (bursa with prop and rein of Chapman).

FIG. 2.—Bursa with abnormally shaped caput (dissection No. 8).

FIG. 3.—Bursa with abnormal caput and ductus seminis aborted (dissection No. 3).

FIG. 4.—Bursa with caput and ductus seminis absent (dissection No. 1).

FIG. 5.—Rudimentary cement glands and blind ductus bursae (dissection No. 3).

FIG. 6.—Small but symmetrical cement glands and nodular spermatheca (dissection No. 6).

FIG. 7.—Branched spermatheca (dissection No. 10).

FIG. 8.—Normal 9th and 10th abdominal segments.

FIG. 9.—Tenth abdominal segment showing each half of the ovipositor widely spread instead of parallel.

a. Caput bursae (bursa copulatrix: Chapman).

b. Prop or hypostema (Chapman).

c. Bursa copulatrix (rein or henia: Chapman).

d. ductus seminis (ductus bursae).

e. Cement gland.

f. Spermatheca or receptaculum seminis.

g. Ovipositor with rods (10th abdominal segment).

h. 9th abdominal segment with rods.

all the internal organs were recognised and appeared to be like those of normal females. In many others the cement glands were recognised and the ovaries, though the ova were swollen up and destroyed. In all sixteen the *bursa copulatrix* with its *caput bursae* was present. In twelve the caput was noticed to be empty, but in two some dark-coloured material was present. The external genitalia were examined in all sixteen. In none was any asymmetry discovered, and in none was any male structure present. In one specimen the two halves of the ovipositor were widely spread instead of lying parallel to one another. This defect was noticed when the insect was captured, and must have been due to an injury occurring shortly after emergence, while the chitin was still soft, or to an error of development (Fig. 9).

I have dissected completely twenty-five undoubted gynandromorphs, for in specimen No. 2 ("Ent. Rec.," xxvi. p. 221) I found androconia in a later search, and can summarise the results as follows. The ovaries were normal and symmetrical in twenty-four, in one they were symmetrical but each ovary had only three follicles instead of four. Departures from the normal number of four follicles in each testis and ovary are rare, except in primary somatic or genetic hermaphrodites. Doncaster has observed six in each ovary in an otherwise normal female *Abrazas grossulariata*. Reduction in the size of the cement glands was noticed twice, and partial abortion of one of the glands in two other cases. Maldevelopment of the spermatheca was also met with. The most noteworthy errors of development occurred in connection with the *bursa copulatrix*, its caput and the *ductus seminis*. It was possible to examine these structures in forty-one gynandromorphs.

Normally the *ductus seminis* arises from the bursa at the same point as the *caput bursae*, or, according to Chapman's nomenclature, at the very commencement of the tubular bursa. In two specimens the *caput bursae* (or, according to Chapman, the entire bursa) and the *ductus seminis* were absent; in a third, the caput (or entire bursa) was absent and the ductus represented by a blind rudiment entering the common oviduct; and in a fourth, though the caput was present the *ductus seminis* was entirely absent. In all these the prop and rein of Chapman were present and normal in appearance. Probably the

abnormalities found in the other specimens would not have interfered with the production of fertile ova, but in these four they must have led to complete sterility. In three specimens, though the caput was present it was abnormal in formation (see figures).

In the thirty-nine specimens, where the point was noted, a variable amount of granular material was seen in the *caput bursae* in twelve, and in some it had become very dark coloured and conspicuous. In twenty-seven the caput was entirely transparent and empty. Of the specimens described in the "Ent. Record," xxvi, p. 221, granular material was present in numbers 4 and 6 and absent in 1, 2 and 3, and it was also absent in the one described in the Journal of Genetics, 1915. In twenty normal females taken as controls, including three *ab. semisyngnatha*, this granular material was noticed in eighteen, it was absent in two. Unfortunately the material was not examined in a fresh condition. Prolonged boiling in potash did not make it transparent. After boiling the caput in several instances was opened and the dark débris was tested but failed to give either Millon's or the biuret reaction for proteids, a failure which is not surprising in view of the treatment to which it had been subjected. The material is probably altered semen, and could only be present in females after fertilisation. If this view is correct, its presence in so few gynandromorphs shows that a much smaller proportion of these had been fertilised than of normal females.

#### PSYCHOLOGY.

Of the psychology of these gynandromorphs I have little information to offer. Their rarity and the enormous numerical preponderance of females over males at Royston makes it very difficult to take any observations.

I have never seen a gynandromorph being courted by a male, nor found one paired. Mr. Newman, with a wider experience, has never seen one courted or paired. Mr. Pickett says he has paid special attention to this point, and in no year has he seen one paired or being courted by a male. There seems to be no physical reason why this should not take place, and only in a very small proportion does there appear to be any anatomical obstruction to fertilisation or oviposition. If my suggestion

about the condition of the bursa be a correct one fertilisation does occur in some of these gynandromorphs, though less often than in the case of normal females.

Since I wrote this I have asked Mr. Bethune-Baker and Dr. Chapman for their opinions. The latter wrote: "As to the dark contents of the bursa I am ignorant, but have supposed it to represent some change (decomposition?) in contents *after* pairing." Mr. Bethune-Baker has noticed its presence, and thinks it is found only after fertilisation.\*

#### EXTERNAL APPEARANCE.

The vast majority of the Royston gynandromorphs show the reduction in wing area accompanied by the presence of blue scales, coarse blue hair scales and androconia on one side only; I have seen more than two hundred of these myself. In most specimens the fore-wing appears to be more affected than the hind-wing, but the reverse may be the case. Occasionally only the fore-wing or only the hind-wing may have the abnormal scales, and the other wing on the same side may show a reduction in size or may appear to be exactly like the one on the opposite side (Pl. LXVII, fig. 2). In some, coarse hair scales are rare and in others androconia. In some the lunules show no reduction in size.

The situation of the blue scales is variable, but they are usually most dense on the part furthest from the thorax and distal to the central spot, or along the posterior border in the fore-wing, and in the hind-wing also they are most abundant in situations distal to the central spot. These are just the situations where blue scaling is not found in the blue females, or where it becomes least abundant.

\* In order to throw light on the nature of the brown material in the bursa copulatrix, I dissected in August 1916 three females of *A. coridon* taken in cop., three virgin females and two gynandromorphs in very fresh condition. Two of fertilised females had the bursa quite full of brown material, which under the microscope appeared amorphous and granular and was mixed with large numbers of living spermatozoa, the third had very little brown material but spermatozoa were abundant. In the virgin females and gynandromorphs there was no granular brown material and no spermatozoa were present. This makes it almost certain that the brown material is only present after fertilisation, and it is probably the secretion of the glandulae accessoriae of the male. The bursal contents of *Ornithoptera helena* gave marked Millon and biuret reactions. The two gynandromorphs, ab. *roystonensis*, showed normal and symmetrical internal and external genital organs.

Blue scaling may be extremely marked as in my specimens (Journal of Genetics, Pl. xxi, fig. 6, and Pl. xxii, fig. 7), or very scanty as in a specimen in Mr. T. W. Hall's collection, which has about fifty blue scales with a few androconia near the apex of the small fore-wing. I have another specimen showing reduction in size of the wings on the right side, especially of the hind-wing. It has only four blue scales and no androconia on the fore-wing, but there are a few additional blue scales on the hind-wing with one or two coarse hair scales and some androconia (Pl. LXVIII, fig. 1).

Another with only a small patch of blue scales, coarse hair scales and androconia is No. 17, and here there is reduction in size of the hind-wing with no abnormal scales (Pl. LXVIII, fig. 2). From these the transition is only a slight one to specimens such as Pickett's (Journal of Genetics, Pl. xxii, figs. 11 and 12) and to the specimens No. 18 and 19. These have the reduced size, but no androconia. Only one or two blue scales are present, but they lie in those areas where blue scaling is commonest in gynandromorphs and only present in the bluest normal females. They are, however, rather dark specimens with but few basal blue scales. In No. 18, too, there is a single blue hair scale. Mr. Pickett possesses a specimen of ab. *semi-syngrapha* with no androconia and no coarse hair scales, but with marked difference in size on the two sides. No. 21 is quite remarkable; it shows no sign of faulty expansion, and yet there is marked difference in the size of the wings on the two sides, and with it a marked reduction in the size of the lunules (Pl. LXIX, fig. 2).

I think that these very unusual specimens are really of the same nature as the others, but the evidence of their gynandromorphism is masked. The reduction in size is a remarkable feature. In *A. coridon* the male is considerably larger than the female, and in the six or seven halved or nearly halved gynandromorphs recorded, the male side has been larger than the female. Yet in the predominantly female gynandromorphs of Royston the side showing male characters is smaller and, as a rule, the more marked the male characters are the greater is the reduction. Local areas which show many blue scales show parallel reduction in size, and so lead to deformity of wing, such as blunting of the apex, curving of the costa or indentation of the margin of the wing.

In addition to the specimens showing male characters and reduced size on one side only, there are a few examples known which show them on both sides. Some are figured here, others in the *Journal of Genetics*. All the forms known so far can be classified in the following way:—

### I. *Unilateral or halved Gynandromorphism.*

(a) Both wings reduced, blue scales, coarse blue hair scales and androconia present. It is not very unusual to find no hair scales and no androconia on the hind-wing.

(b) Fore-wing or hind-wing alone showing the abnormal scales; the other wing usually reduced, but sometimes normal in size.

(c) Both wings reduced, androconia absent. Only one or two blue scales present, and either none or one or two coarse hair scales.

(d) Wings reduced; no abnormal scales present.

### II. *Bilateral Gynandromorphism.*

(a) All four wings affected, but generally unequally (*Journal of Genetics*, Pl. xxii, figs. 8 and 9). Another specimen similar to fig. 8 is in Mr. P. M. Bright's collection.

(b) Three wings affected (Pl. LXVI, fig. 1). This is in Mr. Pickett's collection taken at Royston 1915, and in addition to blue scales it has coarse blue hair scales on both fore-wings. Androconia are numerous on the left hind-wing, uncommon on the right fore-wing and very scanty on the right hind-wing.

(c) Two wings affected (Pl. LXVI, fig. 2). Taken by Mr. Leeds at Royston, 1915. Blue scales not very numerous. Only one or two coarse hair scales, and only one androconial scale seen on each fore-wing. No inequality in size.

(d) Reduction of size on one side; blue scales, coarse hair scales and androconia on the other (*Journal of Genetics*, Pl. xxii, fig. 10).

### III. *Crossed Gynandromorphism.*

Specimen taken by Mr. Pickett at Royston, 1915. Reduction in size with presence of a number of blue scales, coarse hair scales and androconia of left fore-wing. Reduction of size with presence of numerous blue scales and androconia of right hind-wing (Pl. LXVII, fig. 1).



A very important point to consider is the condition of the general somatic characters on the two sides of the body in these blues. Examination of a great number of specimens has convinced me that they are almost invariably the same.

Females of *coridon* vary in colour on the upperside from pale brown to almost black. Some have the spot ringed with white ab. *albicincta*, Tutt, others have whitish spots internal to the lunules, and the amount of blue at the base of the wings is very variable. However marked any of these characters may be in a gynandromorph they are present on both sides alike. The ground-colour of the underside also is variable, but as in normal specimens so in gynandromorphs it is the same on both sides. I have one a peculiar silvery white on both sides, and another of a most unusual chocolate brown colour on both the gynandromorphous and the normal sides.

Spotting often shows slight asymmetry in normal females, and slight asymmetry is still commoner in gynandromorphs, owing to the difference in size and shape of the wings on the two sides; but here again the pattern is approximately symmetrical.

I have three specimens ab. *parisiensis*, Gerh., on both sides, one with basal spots obsolete, ground-colour pale grey and a strong brown line near the margin on both sides, and another is a well-marked example of ab. *crassipuncta*, Court., on both sides. Two specimens figured show great asymmetry, but the difference in size is so marked that it can probably be put down to this cause and not to a real difference of somatic constitution on the two sides. The only specimen I have seen in which the difference is such as to make me suspect a true segregation of somatic characters, heterochroism, is figured in the Journal of Genetics (Pl. xxii, fig. 12). There is great difference in size, which makes one suspect that it is a gynandromorph, though I know one instance of simple heterochroism where the asymmetry of size is equally great. The presence of a blue scale on the small side still further suggests a segregation of secondary sexual characters.

The most striking proof of the identity of somatic constitution on the two sides is afforded by the specimens of ab. *semisygrapha*, Tutt, which show gynandromorphism. My own specimen is figured (Journal of Genetics,

Pl. xxii, fig. 14*a*). A second was captured by Mr. H. B. Williams at Royston, in 1915, and has androconia on both wings on the right side (Pl. LXX, fig. 2), and a third, taken by Mr. F. W. J. Jackson at the same time and place, also has androconia on the small misshapen side (Pl. LXX, fig. 1).

#### THEORETICAL DISCUSSION.

A good deal of evidence has accumulated to prove that sex and secondary sexual characters are Mendelian unit characters, and that although closely linked they are probably separable. There is even some evidence to show that the secondary sexual characters themselves may be separable into more than one unit character. It is thought that the character for sex is carried by a special chromosome sometimes recognisable microscopically, and that secondary sexual characters are probably carried by the same chromosome. It is probable that ordinary gynandromorphs are produced by unequal chromosome divisions at the first cleavage of the normally fertilised ovum, and that in this unequal division both the units for sex and for secondary sexual characters participate. Hence such individuals are likely to be true genetic hermaphrodites, having the gonad, external genitalia and secondary sexual characters peculiar to one sex on the one side, and those peculiar to the other on the other side.

In the Royston gynandromorphs the condition found is quite different from this. In the considerable number examined the gonads, internal and external genitalia have always proved to be female. The dissimilarity on the two sides is confined to certain secondary sexual characters, male scent scales or androconia, coarse blue hair scales and blue scales of ordinary shape, all of which together may perhaps be a single Mendelian character. The irregular division, which I suppose to be the cause of this, must be confined to that part of the chromosome bearing this character. The factor for sex in the chromosome must be unaffected because both gonads are female and are invariably equal in size on the two sides. There is some evidence that the unit for the accessory internal genitalia and for the external genitalia is independent of that for the gonads and it must also be unaffected; for, although the internal organs are occasionally imperfectly

formed, they are always wholly female and almost always symmetrical. In the two specimens in which one cement gland was smaller than the other, in one it was smaller on the gynandromorphous and in the other and more marked example it was smaller on the normal purely female side.

It is difficult to explain why reduction in size takes place on the side showing male characters in an insect in which the male is considerably larger than the female. Large size may be a unit character independent of that responsible for the peculiar scales of the male; but, even if this be so, it remains obscure why the parts which show a mixture of secondary sexual characters should show an actual deficiency of growth. All the other parts on the gynandromorphous side, such as the antennae, legs, abdominal rings and external genitalia, show a normal growth. It is evident, however, that defective growth of the wings is almost a constant feature of the Royston gynandromorphs, and on the whole is most marked where the male element is most manifest. The most notable exception is the specimen (Pl. LXXIII, fig. 5) in the possession of Mr. P. M. Bright. In this the male element, judged by the abundance of blue scales, is stronger than in any other specimen of this kind which I have seen. There are, however, very few androconia; large areas being entirely destitute of them. The wings are equal on the two sides and so it does not fall under *ab. roystonensis*, though obviously it ought to do so. It is interesting to compare this specimen with the next bluest specimen I have seen, in which androconia and coarse hair scales are very abundant on the fore-wing, which is correspondingly small (Pl. LXXIII, fig. 4).

Halved or nearly halved gynandromorphs of *A. coridon* (genetic and primary somatic hermaphrodites) are extremely rare, and only about half a dozen have been recorded. One from Dover, perfectly halved, is figured in Barrett's "British Lepidoptera," vol. i, Pl. xii, fig. 1e. Another was taken by Mr. Quarrington in the Reigate district on July 31st, 1911, and has not been recorded previously (Pl. LXXIII, fig. 3). The external genitalia are partly male and partly female. In a specimen taken at Purley by Mr. Kirkman, the abdomen and three wings are apparently male, and one fore-wing and half the thorax are female (Ent., xxv, p. 2, Pl. i, fig. 3). In these and similar

specimens the male wings are considerably larger than the female, contrasting strongly in this respect with the secondary somatic hermaphrodites, which form the subject of this paper.

The fact that the somatic characters are almost invariably the same on both sides in these gynandromorphs from Royston is important, because it disproves the view that either fertilisation of an ovum by two spermatozoa or fertilisation of one half of a prematurely divided ovum gives rise to the condition of gynandromorphism; though both suggestions have been advanced at one time or another to explain ordinary halved gynandromorphism. An irregular division of chromosomes at the first cleavage of the fertilised ovum may account for the halved examples of gynandromorphous *coridon*, but will not account for bilateral or crossed forms. In these far rarer specimens an irregular division probably took place earlier, perhaps at the second maturation division before the fertilisation of the ovum. In all cases there is probably some antecedent abnormality of the chromosome.

In the majority of lepidopterous insects the female is a heterozygous dominant for sex, the male a homozygous recessive, and *A. coridon* is probably no exception. The occurrence of aberrations peculiar to the female, such as abs. *tithonus*, Meig. (*syngrapha*, Kef.), and *semisyngrapha*, Tutt, supports this hypothesis. In the simpler cases of this kind the spermatozoa always have sex chromosomes of one kind, but the ova are of two kinds: one with a large sex chromosome, which on fertilisation produces a female, the other with a small sex chromosome, which produces a male. If we suppose that some part of the large sex chromosome is lost either before or after fertilisation, femaleness may be incompletely dominant. A somewhat similar condition may exist in the case of the chromosomes bearing the secondary sexual characters, and loss of part of the dominant chromosome (that for female secondary sexual characters) may cause an imperfect dominance of female over male secondary sexual characters. If the dominance becomes much reduced, the male element may become visible in the form of numerous blue scales and androconia. If the margin is narrow, it may only be visible in the form of a few blue scales and androconia; or, where there is almost a perfect balance between the male and female elements, only one or two

blue scales may show the mixed characters, or only the curious deficiency of growth which the mixing seems almost uniformly to produce. And since the deficiency of growth is greatest where the female element predominates least strongly, it is possible that when the balance is very even the chromosomal abnormality may be present without any external evidence whatever. Such an individual might appear to be a normal female *coridon*.

That a gynandromorphous constitution may be masked in this way is suggested by some of the families of *Lymantria dispar*  $\times$  *L. dispar* var. *japonica* bred by Goldschmidt. In several of these families the percentages of males, females and gynandromorphs was such that he was driven to the view that some of the specimens which appeared externally to be males were really gynandromorphs.

We are thus met by the paradox, that in *Lymantria* and *Agriades* gynandromorphs exist with the external marks of their gynandromorphism entirely masked.

I venture to hope that by putting forward these very speculative suggestions I shall stimulate some more competent than myself to undertake the work necessary in order to prove or disprove them. Field observations may fill in some of the gaps in our knowledge, but breeding experiments and cytological investigations are needed to solve the fascinating problem presented by the Royston gynandromorphs.

In conclusion, I offer my thanks to many Entomologists for helping me, and to Messrs. Jackson, Leeds, Pickett and H. B. Williams for permission to photograph and figure their specimens.

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## EXPLANATION OF PLATES LXV-LXXIII.

## PLATE LXV.

- FIG. 1. Gynandromorph resembling ab. *inaequalis*. Wings on left side reduced in size. Numerous androconia and coarse hair scales on blue striped areas of left fore-wing.
- FIG. 2. Gynandromorph showing reduction in size of wings on right side, numerous blue scales, coarse hair scales and androconia, and curving of costa of fore-wing.

## PLATE LXVI.

- FIG. 1. Bilateral gynandromorphism. Blue scales and androconia on right fore-wing, right hind-wing and left hind-wing (Pickett coll.).
- FIG. 2. Bilateral gynandromorphism. Blue scales and an androconial scale on each fore-wing (Leeds coll.).

## PLATE LXVII.

- FIG. 1. Crossed gynandromorphism. Blue scales and androconia with reduction in size in left fore-wing and right hind-wing (Pickett coll.).
- FIG. 2. Fore-wings equal and normal. Left hind-wing with reduction in size, blue scales and androconia (Dissection No. 7).

## PLATE LXVIII.

- FIG. 1. Gynandromorph with reduction in size of both wings on right side. Four additional blue scales and no androconia on right fore-wing, and a few additional blue scales, two coarse hair scales and a few androconia present on right hind-wing.
- FIG. 2. Gynandromorph with reduction in size of both wings on right side. A few blue scales, coarse hair scales and androconia near posterior border of right fore-wing, but none present on hind-wing (Dissection No. 17).

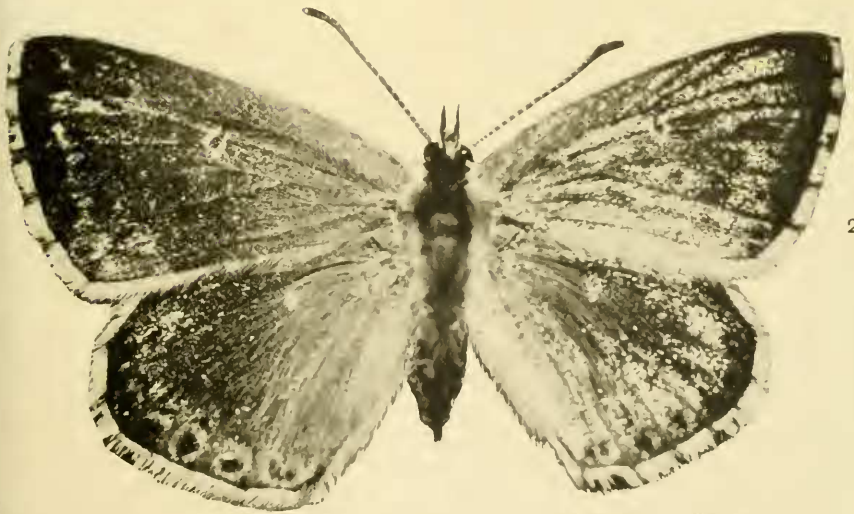
## PLATE LXIX.

- FIG. 1. *A. coridon* ab. *semisyngnatha*. Wings on right side reduced in size. Costa of right fore-wing curved. A few additional blue scales but no androconia and no coarse hair scales on right side.
- FIG. 2. Wings on left side reduced in size and with smaller lunules. No blue scales and no androconia present (Dissection No. 21).





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